THE ARMOURED DINOFLAGELLATA: I. PODOLAMPIDAE

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With 18 Text-figures

The present work including the drawings, based on materials collected by surface hauls from the offshore and inshore waters near Shimoda facing Sagami Bay in 1936–1937, had been finished in 1940 and was rewritten recently to be published here. A powerful branch of the Kuroshiwo flows into Sagami Bay. We can observe, then, some tropic and subtropic species even in the materials collected in Shimoda Bay.

Family **Podolampidae** (SCHÜTT)

Podolampinae SCHÜTT 1896: LEMMERMANN 1906: KOFOID 1907.
Podolampaceae LINDEMANN 1928, 1937: BALECH 1963.

The family Podolampidae is characterized by entire lack of cingular structural differentiation and by peculiar arrangement of the thecal plates. KOFOID (1909), finding a single, nearly empty theca of *Podolampas elegans* in a winter plankton sample from Naples, gave detailed accounts of its thecal morphology, and fairly recenty BALECH (1963) made an analytical study of the thecal elements of some species, though with incomplete results.

Two genera of *Blephalocysta* and *Podolampas* are involved in the family. In regard to general body shape, the former resembles some species of *Glenodiniopsis* or *Sphaerodinium*, while the latter to some species or groups of the Family Peridinidae. Both *Blephalocysta* and *Podolampas* agree with each other in their plate formula, and this appears to suggest some systematic affinity between the Families Podolampidae and Peridinidae as illustrated in Diagram A. It may be of no use to explain them here because readers can easily realize it visually. BALECH's figures seem to agree in the main with my interpretation but not KOFOID's, and yet BALECH accepted KOFOID's plate formula which differs much from mine as described below.

SCHÜTT (1895) regarded a postmedian series of three plates as representing the girdle, while KOFOID designated them as the postcingulars, postulating that the post-marginal portions of the premedian plates as representing "a

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rudiment of the girdle". LEBOUR (1925) and LINDEMANN (1928) also followed KOFOID's interpretation. KOFOID's analysis is far reaching but incomplete, and if he had made a comparative study of the two genera involved in the family, he would have been obliged to change his interpretation which has been accepted even to this time by SCHILLER (1931) and BALECH (1963).

Blephalocysta agrees with *Podolampas* in the total number of their thecal

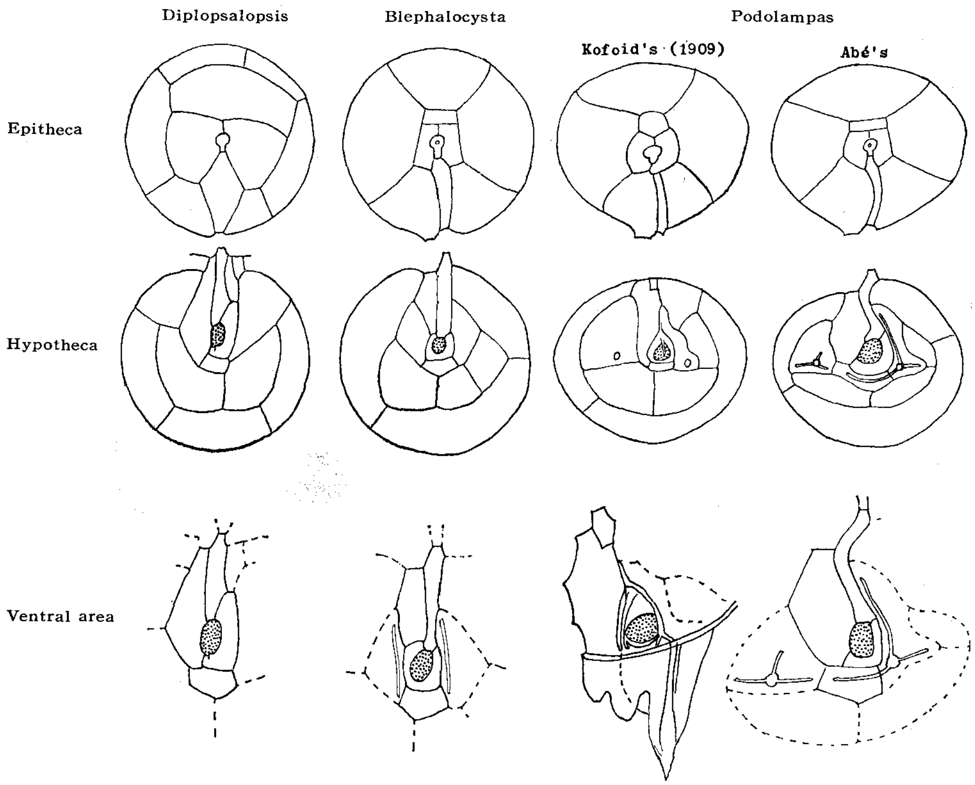


Diagram A. Homology in plate patterns of epitheca, hypotheca and ventral area of *Diplopsalopsis, Blephalocysta* and *Podolampas.* To be free from any prejudices, none of the abbreviated signs of plate formula is given here and the cingular plates of *Diplosalopsis* are also expelled out of the drawing. As to the genus *Podolampas,* KOFOID's (1909) three figures are cited here. Concerning the ventral area, the sulcal plates are figured in solid lines and others in broken lines after the present author's new interpretation.

plates. They differ from each other, however, in plate arrangement and structural differentiations of their hypotheca. Here, one has to re-examine the two genera plate by plate, standing on an unprejudiced point of view. The plates bordering the apical pore and its ventral extension are to be included in the apical series. Not only the pore itself but also its ventral extension is covered, in this case, with a single pore plate (Fig. 21, 24 & 27).

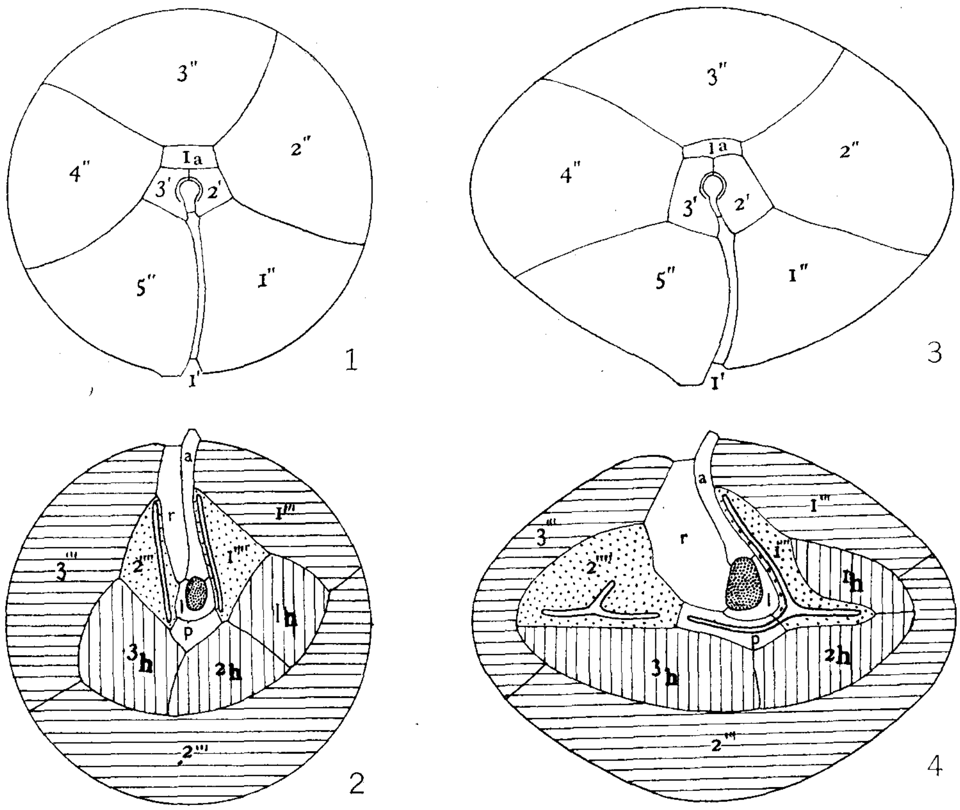
Here one can see two small plates on either side of the pore and another slender plate extending ventro-posteriorly from the ventral end of the pore. All of these three plates are really the apicals. On the dorsal side of the pore is a small plate which seems to be an apical element in *Blephalocysta* but is much dislocated postero-dorsally from the pore in *Podolampas* (Figs. 46, 57 & 62), showing at the same time some structural differentiation as given in Fig. 14. Five larger plates of KOFOID's six precingulars are in reality homologous to the precingulars of *Peridinium* and its allied genera (Diagram A).

KOFOID (1909) imagined "a missing girdle" along the posterior margins of these five plates, basing his idea on some structural differentiation which could not be confirmed by the present author who, however, agrees with him in regarding them functionally as representig the bed for the transverse flagellum, because of a different structure to be given later.

The present author consents to KOFOID's opinion as to the post-cingular plates. Before going further, one has to define clearly the exact exent of the ventral area and its thecal elements. As to this point one must remember that the ventral area of *Peridinium* and all genera of Dinophysidae* consists of four plates lying around the flagellar pore. In *Blephalocysta*, the pore is encircled almost completely by a minute, U-shaped plate. A narrow plate from the posterior end of the ventral apical (Figs. 13, 28 & 29) extends to the anterior slit of the U-shaped plate. There are two other plates, one along the right of the narrow one and the other on the postero-dorsal side of the pore. All four of these plates agree in lying directly or indirectly around the flagellar pore and also in lacking any distinct surface extension. They represent in all probability the sulcal elements. In all of the genera cited above, subsulcal lists stand basally, not on any of the sulcal plates, but on the plates directly bordering the ventral area. In this respect it is to be taken into consideration that in *Podolampas* the bilaterally located wing-complex, particularly its solid spinous structure stands basally on the plate corresponding to the list-bearing one of *Blephalocysta*. It is to be recollected in this respect that in the *Steinii*-group of *Peridinium*, the antapical spinous appendages stand invariably on the antapical plates (KOFOID 1909). If the abovo-mentioned comparative study is accepted as reasonable, these list-bearing plates of *Blephalocysta* and spine-bearing ones of *Podolampas* are to be designated as typical antapicals, though they are separated bilaterally. In consequence, the other three plates, arranged bilaterally in the postero-dorsal in *Blephalocysta* but taking a J-shape arrangenent in *Podolampas* (two on the dorsal and one on the posterior left ventral), are homologous to the hypothecal or posterior intercalary plates and are so defined here (Diagram A, Figs. 1, 2, 4, 13, 25, 36-38, 54 & 64).

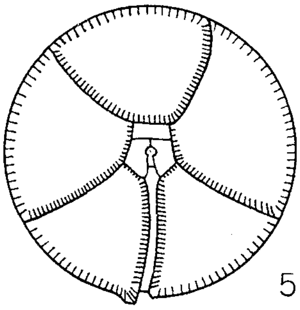
* In press.

All of the four sulcal plates have no surface extension in *Blephalocysta*, but in *Podolampas spinifera* its posterior-most element is furnished with an antapical spine and median parts of its lateral wings. Further, in all of the dispinous species of *Podolampas* (Figs. 13, 44, 54 & 64) the plate is furnished with only a distal major part of the median wing of the left antapical appendage. In this connection, it must be noted first that the surface of the



Figs. 1–4. Plate arrangements of *Blephalocysta* and *Podolampas* : Fig. 1. The epitheca in apical view of *Blephalocysta*. Fig. 2. The hypotheca in antapical view of *Blephalocysta*. Fig. 3. The epitheca in apical view of *Podolampas*. Fig. 4. The hypotheca in antapical view of *Podolampas*. Plate formula of hypotheca is shown by different markings in Figs. 2 & 4.

thecal plates covering the ventral area in all subgenera of *Ceratium* is invariably furnished with reticulated structures which are as distinct as on the general body surface. This is presumably caused by that these plates are laid entirely outside the flagellar slit, along which the trailing flagellum is extending. Then secondarily it must be noticed that the ventral area of *Peridinium* species belonging to the group Avellana (Abé 1936) is narrow and deep trough-shaped as a whole and their four sulcal plates are easily distinguishable from other thecal plates by their surface structure. In *Peridinium pentagonum* or its allies, however, the ventral area is differentiated into an anterior narrower and sharply indented sulcus, which is covered with only the anterior and the left sulcal plates, and an extremely broader posterior portion which is covered with the right smaller and the posterior much larger sulcal plates. In this case, the surface of the posterior sulcal plate is furnished with distinctly reticulated structures just similarly as in other thecal plates due presumably to independency of the posterior plate from activity of the trailing flagellum. The sulcal origin of this plate will be as-



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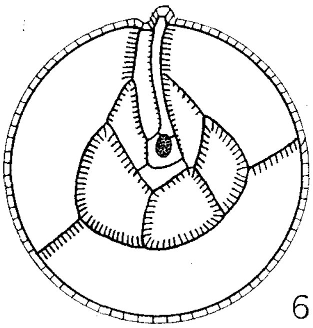

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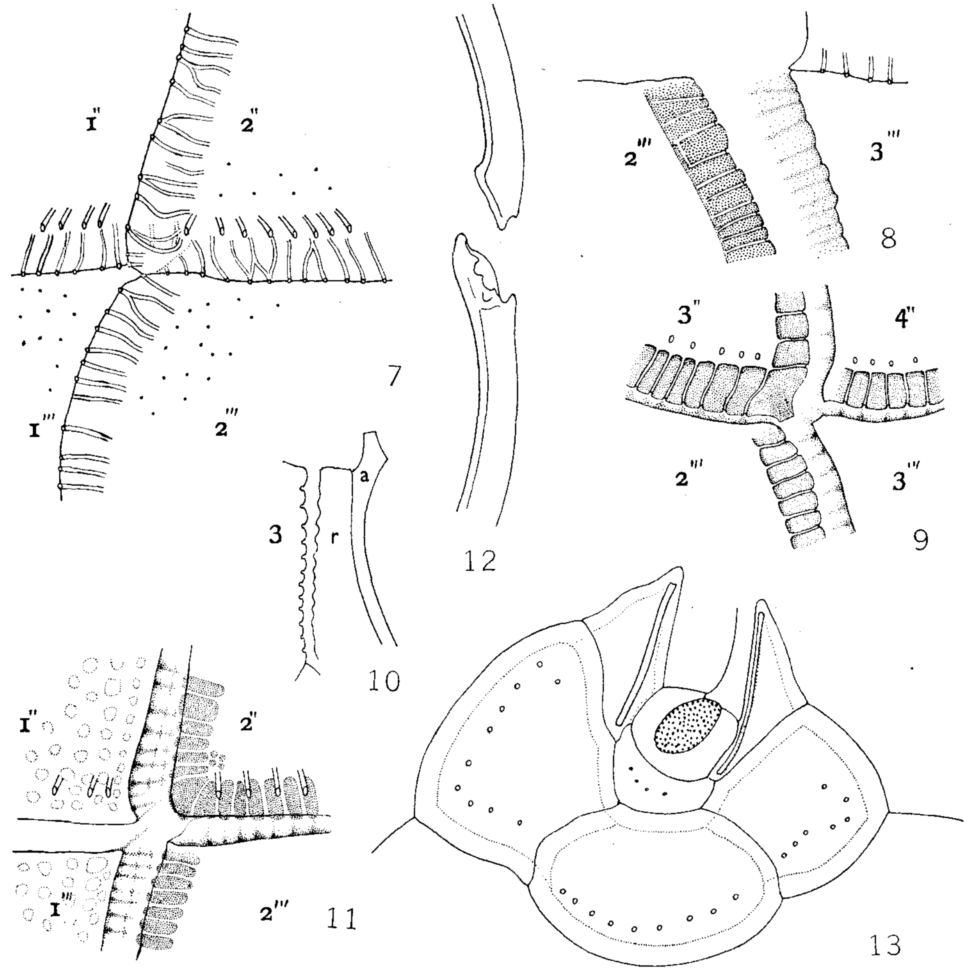
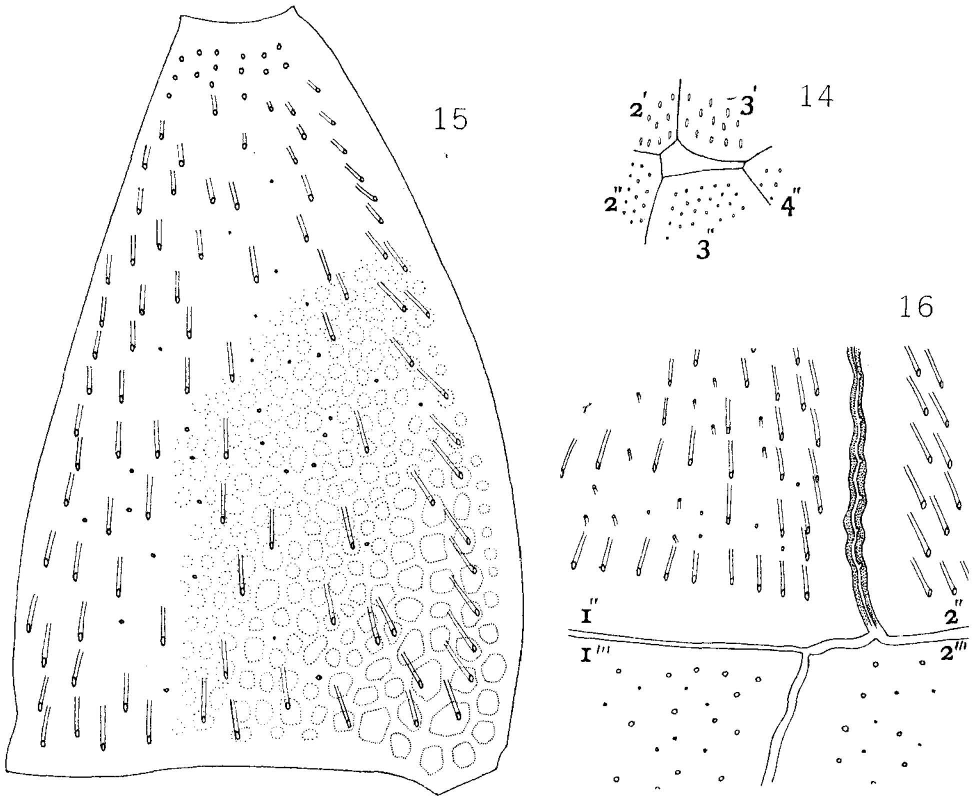
Figs. 5–6. Distributions of slanting contact faces between adjoining thecal plates in *Blephalocysta* : Solid lines represent surface sutures between adjoining plates and zones of short parallel lines along a side of the solid line represent the so-called "band of striae", that shows the side toward which the face of contact is slanting down. Fig. 5. Epitheca. Fig. 6. Hypotheca.

certained only when the detailed comparative studies on many species of *Peridinium* are completed. Basing on these and other unpublished facts observed and also judging from the fact that the cingular flagellum adheres along its entire length to the cingular wall whereas the whole trailing flagellum is liberated at the root, the present author has become clinging to the supposition that the posterior sulcal plate is the first to acquire the properties of the general body surface. As referred later in detail, the formation of filopodia and reticulipodia from the surface of the hypotheca in *Podolampas* is most probably effective to enhance the buoyancy of the bodies without any kinds of marked surface extensions. The antapical list bilaterally



Figs. 7–13. Fig. 7. Intact surface view of a part of thecal surface of *Blephalocysta Okamurai*, showing arrangement of canaliculi lying along slanting faces of contact and a row of particularly differentiated pores with their inwardly extending tubules, arranged along the posterior submarginal parts of two precingular plates. Fig. 8. Completely separated two postcingular plates, each with structural differentiations respectively on the inner surface of the overlapping edge and on the outer surface of underlying edge of the adjoining plate. Fig. 9. Slightly separated four plates of another speciment of *B. Okamurai*, showing the confronting arrangement of thin lighter lines on the under-surface of the overlapping edge and thin darker lines on the outer surface of the underlying edge of its adjoining plate. Fig. 10. Anterior portions of two sulcal plates and a median end of the right ventral postcingular plate, separated a little from the sulcal ones. A line of sutural pores is not seen on either side of the anterior sulcal plate in this case. Fig. 11. Slightly separated four plates corresponding to those shown in Fig. 7, but of a different specimen. The direction of slanting face of contact along a longitudinal suture is reverse to that shown in Figs. 8 and 9. Fig. 12. Optical cross-section of slightly separated two plates, showing the J-shaped contact faces between the two adjoining plates and the structural differentiation found on respective confronting faces. Fig. 13. The posterior half of the ventral area and three hypothecal intercalary plates of *B. Okamurai*. It may be worthy to give attention to the perforated posterior sulcal plate.

formed on just the dorsal side of the flagellar pore is seemingly effectual to keep the free activity of the trailing flagellum from any obstacles which might be caused by the reticulipodiaformation. Thus activity of the flagellum and reticulipodia can be considered as cooperating against the sinking of the body. The single spined *Podolampas spinifera* agrees well with the other double spined species in these respects, although some taxonomical question

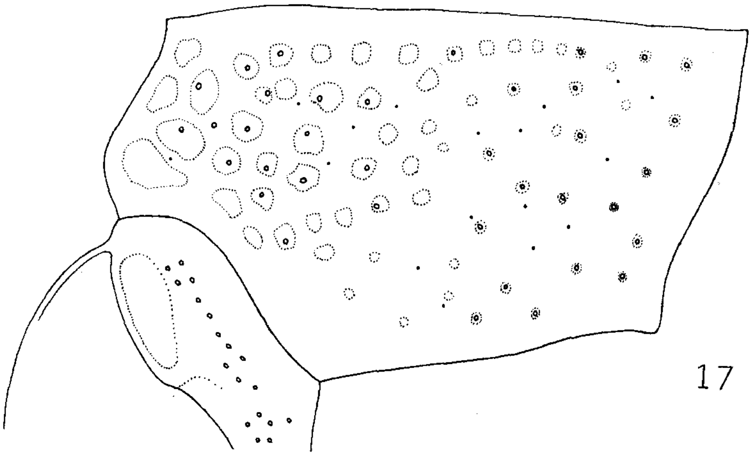


Figs. 14–16. Fig. 14. The non-perforated anterior (epithecal) intercalary plate and its perforated adjacent plates in *P. bipes*. Fig. 15. Regional differences found in the inclination of canaliculi penetrating through the plate wall of an isolated right-ventral precingular in *P. bipes*. Fig. 16. Differences found in the inclination of thecal canaliculi between the precingular and the postcingular rows of plates in *P. bipes*.

is left unsolved about the former.

As one of the characteristics of the family, it is to be noted that the anterior sulcal plate has, at its posterior end, a distinctly elongoted extension which bends dorsally and then anteriorly, to form an antero-median part of the tubular wall opening to the flagellar pore (Figs. 20, 60; BALECH's figures 7, 14, 19, 27, 31, 41 & 42).

There can be distinguished six sorts of pores penetrating through the thecal wall, and each has its own type of distribution. The apical pore and the flagellar pore are included in these six kinds. The third kind comprises minute pores distributed throughout the majority of the thecal plates, with the exception of the anterior intercalary plate of *Podolampas* which is free



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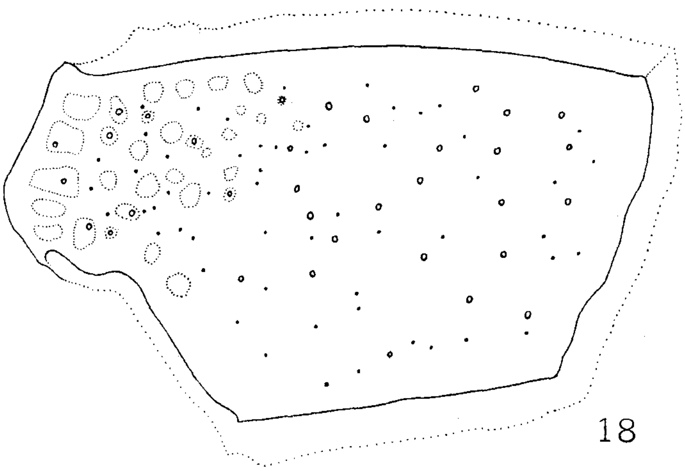

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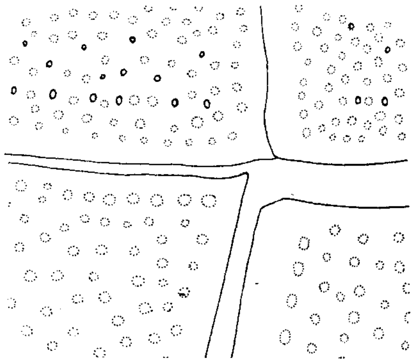
Figs. 17 & 18. Individual variation found in the distinctiveness and distributions of surface poroids and perforations in the left postcingular plates separated from two different specimens of *P. bipes*.

from any perforation. The outer surfaces of the other thecal plates are generally sprinkled with polygonal poroids of various sizes and of different distinctiveness (Figs. 11, 15, 17–20). These pores are nothing but outer openings of canaliculi which penetrate perpendicularly or obliquely throughout the entire thickness of the thecal plates and open partly within the poroids but partly outsides them. In apical regions, these canaliculi lie in the main perpendicularly to the body surface, but in the more posterior regions of the precingular plates, they are more strongly slanted and open obliquely towards the posterior (Figs. 14, 15, 16).

The face of contact between any two adjoining plates is J-shaped in an optical section (Figs. 12, 20); that is, a knife-edged margin of one plate is underlaid with another knife-edged margin of the adjoining plate. Along this face of contact are arranged sub-equidistantly a line of canaliculi, opening perpendicularly to the body surface but obliquely to the inner surface of the thecal wall. This corresponds to KOFOID's (1909) "band of striae". By sliding apart two plates in contact for a short distance, it can be visualized that transverse darker broad zones alternate with very thin lighter striae either on the under-surface of the overlapping margin (Figs. 9, 11) or on the outer surface of the underlying margin (Fig. 20). These lighter striae correspond to the site of the strongly slanting canaliculi, along which the thickness of the marginal wall is diminished. On the other hand, one can often discern darker thin striae similarly arranged on the surface of the opposite knife-edged margin; they are thickest at their proximal ends and become fainter towards the distal end of the margin. These darker thin striae are in reality due to slight thickenings on the margin surface and form, together with thin lighter striae on the opposite margin surface, tubular structures of the canaliculi (Figs. 9, 10, 20 r).

The fifth sort of pore is represented by serially arranged pores or canaliculi which are seen only in the post-submarginal zone of the postcingular plates (Figs. 7, 9, 11, 20, 21 & 23). It is noteworthy in this connection that the transverse flagellum of armoured dinoflagellates is generally ribbon-shaped and sticks to the bottom of the girdle along its inner and thinner side, and it is often reported that there is a line of pores along the bottom of isolated cingular plates of *Ceratium*, *Peridinium* and other genera. I have ascertained in *Ceratium* that the circular flagellum will instantly be shortened and becomes motionless as soon as it is separated from the cingular wall, while the other trailing flagellum is still in active motion. This supports the view that the circular flagellum can move actively so far it is connected with the intramembraneous protoplasm along its entire length, presumably through the linearly arranged pores seen along the bottom of the cingular plates. The present author's supposition is that the circular line of pores arranged in the posterior submarginal zone of the precingular plates corresponds to that found along the bottom of the cingular wall in other genera.

The sixth and last sort of pore is the double band of pores or the "pore band" according to KOFOID (1909),differentiated only in *Podolampas* (Figs. 55, 58, 59, 61, 64, 65 & 67 *2''''*). It consists of rather large pores arranged along



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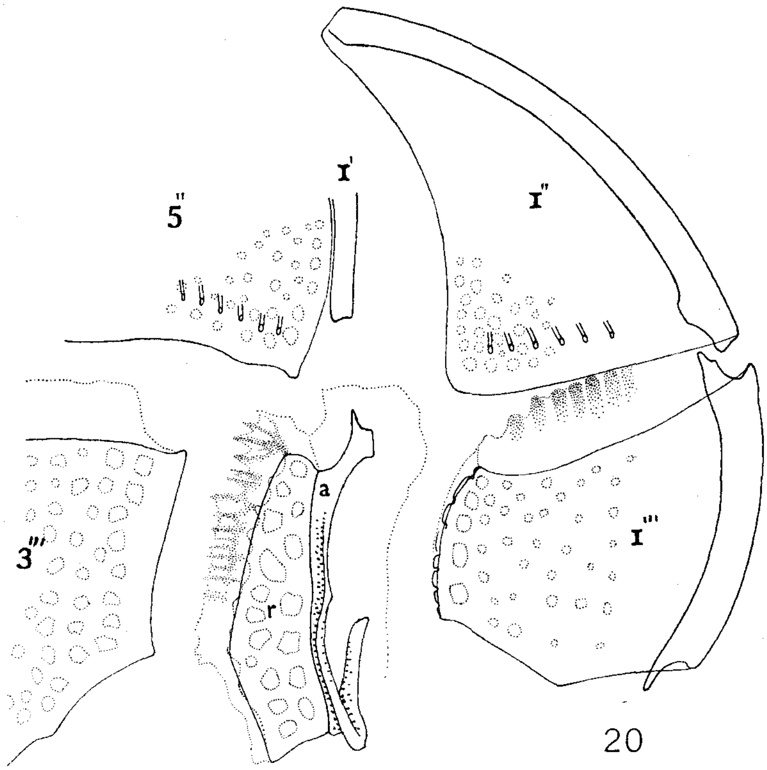

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Figs. 19–20. Structural differentiations of thecal plates in *Blephalocysta Okamurai* : Fig. 19. Left ventral equatorial portion including two precingulars and two postcingulars. Surface areolation is well differentiated but the particular row of larger pores is scarecely distinguishable. Fig. 20. Undisjoined anterior two sulcal plates and their adjacent plates partly or entirely disjoined. Trough-like concavity along the surface of the anterior sulcal and well built surface areolation of the right sulcal plates can clearly be appreciated. The specially differentiated precingular row of pores, the optical cross-section of the J-shaped disjoined two faces of contact, and the structural differentiations found on the two underlying edges, one belonging to the left ventral postcingular and the other to the right sulcal plates, are also illustrated.

the anterior submarginal regions of the three hypothecal plates and the right antapical plate, in which the pore band shows a peculiar zigzag course terminating at the postero-median corner of the plate. STEIN (1883) called these pore bands "peculiar comb-like furrows" and KOFOID (1909) analyzed them for the first time, but incompletely, and failed to elucidate their morphological and functional significance. In this regard, a great stress should be put on SCHÜTT's work (1899) reporting capability of forming an extramembraneous protoplasmic layer and an extension and retraction of radial filopodia and laterally or posteriorly extended reticulipodia issued from the posterior half of the body of *Podolampas bipes* and some other dinoflagellates such as *Prorocentrum*, *Ceratium*, *Peridinium* and *Ornithocercus*. The existence of the extramembraneous protoplasmic layer, filopodia and reticulipodia outside the tightly encrusting thick thecal wall, and further the inward or outward passage of these protoplasmic structures cannot be understood without taking into consideration the perforation of the thecal wall, prevalently seen in armoured dinoflagellates. In the antapical view of *Podolampas*, it can be seen that the so-called pore band is arranged so as to keep certain distance from the bilaterally standing winged appendages along its major length, except for the right ventral where the band is far removed from the flagellar pore. Resultantly, even if the filopodia or reticulipodia are extruded actively from the pores of the pore band, they will not disturb very much the effective movement of the trailing flagellum. The arrangement and extension of the antapical wings also seem to lend support to this view. The entire lack of surface extensions such as cingular lists, laterally extending spines or wings in Podolampidae, will greatly increase the sinking rate of the body. On the other hand, the formation of filopodial or reticulipodial extensions may then regulate or enhance the buoyancy of the least frictional and simple-shaped forms such as *Podolampas*. In this connection it is noteworthy that long-horned *Ceratium* species begin to sink rapidly into deeper layers of the sea as soon as they lose their horns from their base by regulatory autotomy* or their trailing flagellum is retracted into the body.

Genus *Blephalocysta* EHRENBERG

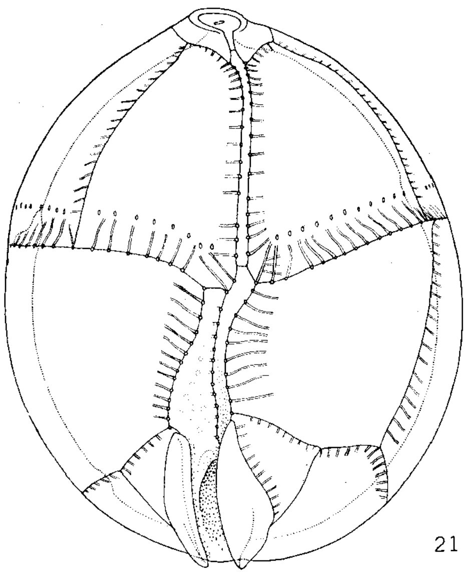
BÜTSCHLI 1889: SCHÜTT 1895, 1896: PAULSEN 1908: KOFOID 1909: LEBOUR 1925: LINDEMANN 1928: SCHILLER 1937: BALECH 1936.

The body is spherical or rotated ellipsoidal without any trace of cingular structural differentiation or of an apical elongation. Bilaterally placed, semicircular lists standing along the posterior half of the ventral area are the sole surface extensions. Arrangement of the thecal plates in typical cases

* Unpublished data.

are illustrated in Figs. 1, 2, 5, 6, and the plate formula is, 3', 1a, 5''', 3p, 3'''' and 4 sulcal plates.

There have been reported four species, *splendor-maris*, *striata*, *Paulseni* and *denticulata*. Their specific distinction, however, is uncertain because detailed, comparative morphological studies are entirely lacking and individual and



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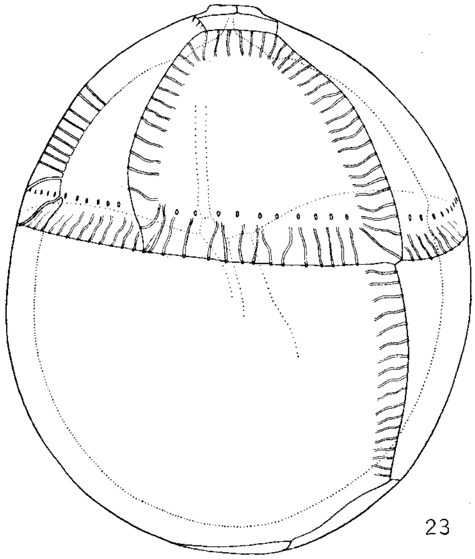

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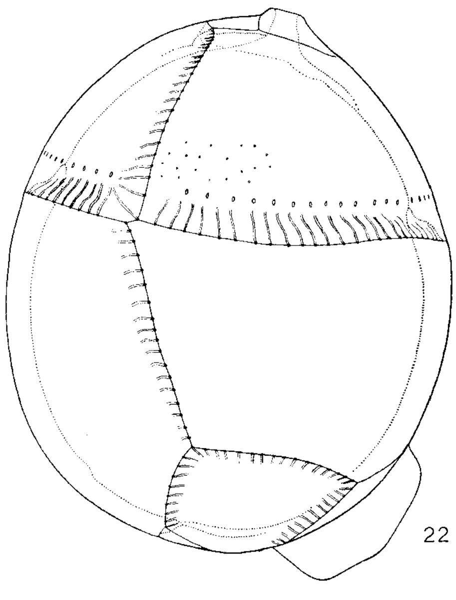

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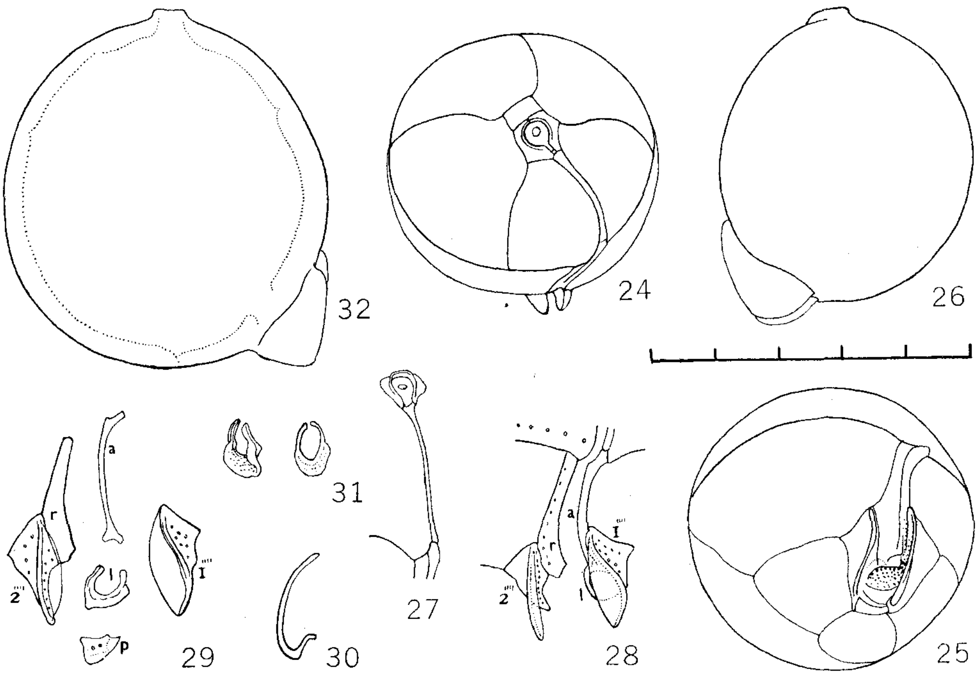
Figs. 21–23. *Blephalocysta splendor-maris* with illustrations of sutural rows of canaliculi and the precingular circular row of rather larger pores: Fig. 21. Ventral view. In this specimen is seen a row of sutural pores along either side of the anterior sulcal plate. Fig. 22. Side view, showing the thickness of the thecal wall and the apical pore opening. Fig. 23. Dorsal view. In the left anterior part of this figure is illustrated an optical section of the wall, together with the penetrating directions of general thecal pores and that of the differentiated precingular row of pores.

species variations are very incompletely known. The present author observed two forms collected in Shimoda Bay; one with a smaller ovoidal body corresponds to *splendor-maris*, and the other with a larger spheroidal body agrees with that reported by OKAMURA from the southeastern off-coastal waters of Japan.

Blephalocysta splendor-maris EHRENBERG

(Figs. 21-32)



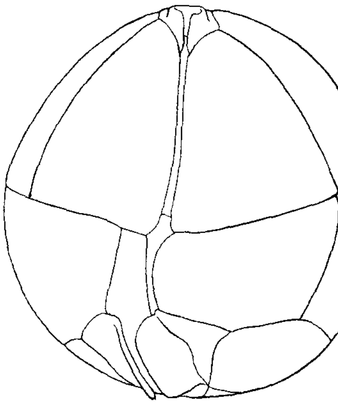
Figs. 24–32. *Blephalocysta splendor-maris* : Fig. 24. Ventral apical view of the epitheca. Fig. 25. Postero-lateral view of the body, showing the ventral area and the three posterior intercalary plates, of which the median is the smallest. Fig. 26. Side view. Fig. 27. The three apical plates together with the pore plate and anterior portions of the two sulcal and the median end of the right ventral postcingular plates, isolated from the other thecal plates. Fig. 28. Anterior three of the four sulcal plates and the two antapicals, split apart along the longitudinal suture passing along the right of the ventral apical and the anterior sulcal plates. Fig. 29. Separated four sulcal plates (a, r, l, p) and the two antapicals, one of which is sticking to the right sulcal one. Fig. 30. Side view of the anterior sulcal plate, arched along the body surface and then along the tubular wall of the flagellar pore-pit. Fig. 31. Ventral and right ventral view of the U-shaped left sulcal plate. Fig. 32. Side view of a rather larger specimen, showing optical section of its thecal wall ; here are shown sites of anteriorly located circular cingular suture and of postcingular-posterior intercalary suture at the antapex. (The scale in this and other figures is for 50μ in total.)

STEIN 1883, Pl. 7, Figs. 17–19; Pl. 8, Figs. 3–5: SCHÜTT 1895, p. 162, Pl. 20, Fig. 61, *1–3, 10, 14, 16–19*; 1896, p. 23, Fig. 24, a, b: BÜTSCHLI 1889, Pl. 53, Fig. 2: PAULSEN 1908, p. 93, Fig. 126: KOFOID 1909, p. 51: LEBOUR 1925, p. 160: SCHILLER 1937, p. 477: BALECH 1963, pp. 16–19, partim, Pl. 3, Figs. 36, 37.

The body, about 1.2 times longer than broad, has its largest transverse diameter at the middle, shortly below the circular sub-equatorial suture which forms descending arcs bilaterally on the ventral and the sutural plain tilts down ventrally as a whole. The anterior or epithecal intercalary plate lies just on the dorsal of the flagellar pore. All of the precingular plates agree in having subequal length. The postcingular row of plates has its greatest length in the mid-dorsal, where it is about 3.5 times longer than in the mid-ventral region. The two antapicals are similar in both shape and extent, while the three posterior or hypothecal intercalaries are dislocated somewhat as a whole toward the left. The left ventral postcingular is much smaller in circular length than the right ventral of the same series, the former corresponding to a right ventral precingular only, while the latter to the two right ventral precingulars. The anterior sulcal plate, sigmoid in shape, has subequal breadth throughout its anterior major length, anteriorly indenting the epitheca for a short distance and posteriorly expanding bilaterally along the anterior brim of the flagellar pore, bending here dorsally and then anteriorly to form the antero-median part of the tubular wall of the hole which opens at the flagellar pore and through which the two flagella pass out. The posterior major portion of this plate is trough-shaped, and the proximal, longitudinally extending portion of the cingular flagellum lies along this trough. The right sulcal plate is irregularly shaped and distributed with surface poroids just as in the case of *B. Okamurai* (Figs. 20, 21). Differing from *Podolompas*, the right sulcal lies separated from the posterior sulcal plate, partly due to the deeply U-shaped left sulcal one and partly owing to the medianward expansion of the right antapical beyond the base of the right subsulcal list in its middle (Fig. 13). The posterior sulcal lies transversely between the two antapicals.

Dimensions; Length, 45–55 μ. Greatest transverse dimension, 40–51 μ.

Figs. 33–38. *Blephalocysta Okamurai*: Fig. 33. Oblique ventral view. Fig. 34. Side view. Fig. 35. Apical view. Fig. 36. Antapical view. Fig. 37. Postero-ventral view, showing thecal surface areolation, the sulcal lists and concaved portion of the sulcus. Fig. 38. Isolated posterior intercalary plates and intact structural relations of the antapicals and the other three sulcal plates. The posterior sulcal (p) is separated from other sulcal members, sticking to the median posterior intercalary. This, together with Fig. 36, shows the decrease in size of the three posterior intercalary plates from right to left. Thickness of thecal wall is shown in Figs. 35 & 36.



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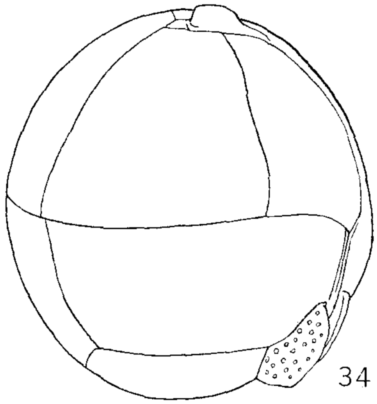

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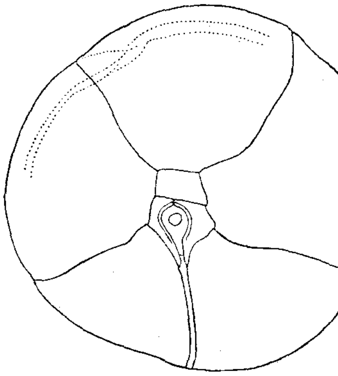

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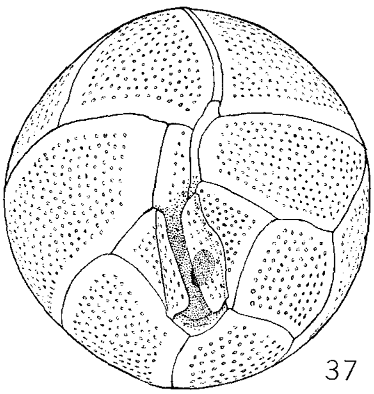

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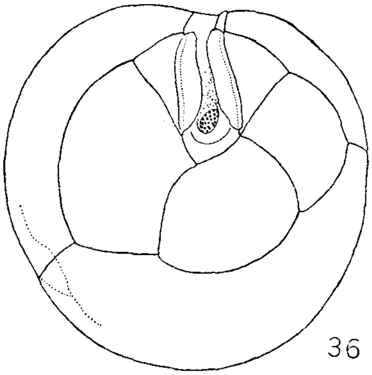

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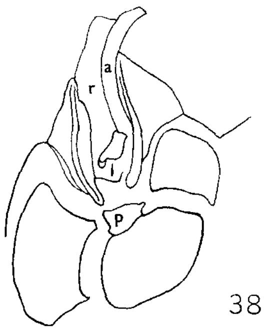


38

Blephalocysta Okamurai n. sp.

(Figs. 33-38)

Syn. *Podolampas splendor-maris*, SCHÜTT, partim, Pl. 20, Fig. 61 *15*: OKAMURA 1907, p. 127, Pl. 5, Fig. 34 a-d: LINDEMANN 1928, p. 101, Fig. 88 a-b: BALECH 1963, partim, pp. 16-19, Figs. 34, 35, 38-44.

The present form agrees with OKAMURA's specimens from Tosa in size and shape of the body, but differs from *splendor-maris* not only in its more rotund body shape but also in the length of the precingulars and postcingulars and further in its more anteriorly located sulcal list. The list is distinctly areolated as are the general thecal plates (Figs. 34, 27), and laid at the middle of the span between the antapical end of the body and the equatorial circular suture which is not so markedly dislocated anteriorly as in the previous species. Being affected by the greater size of the hypothecal intercalaries, the length of the postcingular plates is smaller all around the body. Consequently, the left ventral postcingular is broader than long (Fig. 33). The present species very much resembles *Paulseni* SCHILLER in general body shape and in the decrease in relative size of the three hypothecal plates toward the left. In *splendor-maris* the median one of the three is the smallest. Judging from SCHILLER's figures, *Paulseni* has its circular suture much dislocated anteriorly as in *splendor-maris*, but not so distintly as in the present new species. It is reported that the anterior intercalary is absent in both *striata* and *Paulseni*. However, it is not certain whether the plate is actually undifferentiated or it was overlooked by the authors, because in the majority of observed specimens this plate has not always been analysed so clearly as illustrated in this paper.

Dimensions: Length, 56-63μ. Greatest transverse dimensions, 53-60μ.

Genus *Podolampas* STEIN

GOURRET 1883: BÜTSCHLI 1889: SCHÜTT 1895, 1896: PAULSEN 1908: KOFOID 1909: LEBOUR 1925: LINDEMANN 1928: SCHILLER 1937: BALECH 1963.

The body is broad or elongated pear-shaped with or without dorso-ventral flattening, tapering anteriorly into an apical horn. All the cingular structures or allies are absent. At the posterior end of the body stands an antapical spine supported by two bilateral wings or two bilaterally standing spines each supported by three wings expanding laterally, medially and ventrally. In the latter type with two spines, the ventral wing of the left set bends medianwards in its marginal portion over the left half of the ventral area to cover the flagellar pore, the posterior half of the anterior sulcal plate, and also the anteriorly extending proximal part of the cingular flagellum. The two spines are either separated from each other or conjoined at the median by their median wings. In the monospiny species, the antapical spine and median parts of its bilateral wings stand on the plate corresponding to the posterior sulcal one of *Blephalocysta*, while in the two spined species the median wing of the leftside spine stands bilaterally along the entire transverse length of the plate, and the major parts of the left and the entire set of the right antapical appendages stand respectively on the left and the right antapical plates. If based solely on this observational analysis, one may be liable to regard the small median plate as an antapical element. Comparative studies of the two genera, however, lead us to appreciate the true nature of the median plate as of sulcal origin.

In conforming to the apical elongation of the body, the anterior intercalary plate comes to lie in this genus far posteriorly from the apical end. One of the most peculiar characteristics of this genus is found in the double row of rather larger pores, nearly encircling the base of the antapical appendage with the exception of the midventral portion occupied by the ventral area.

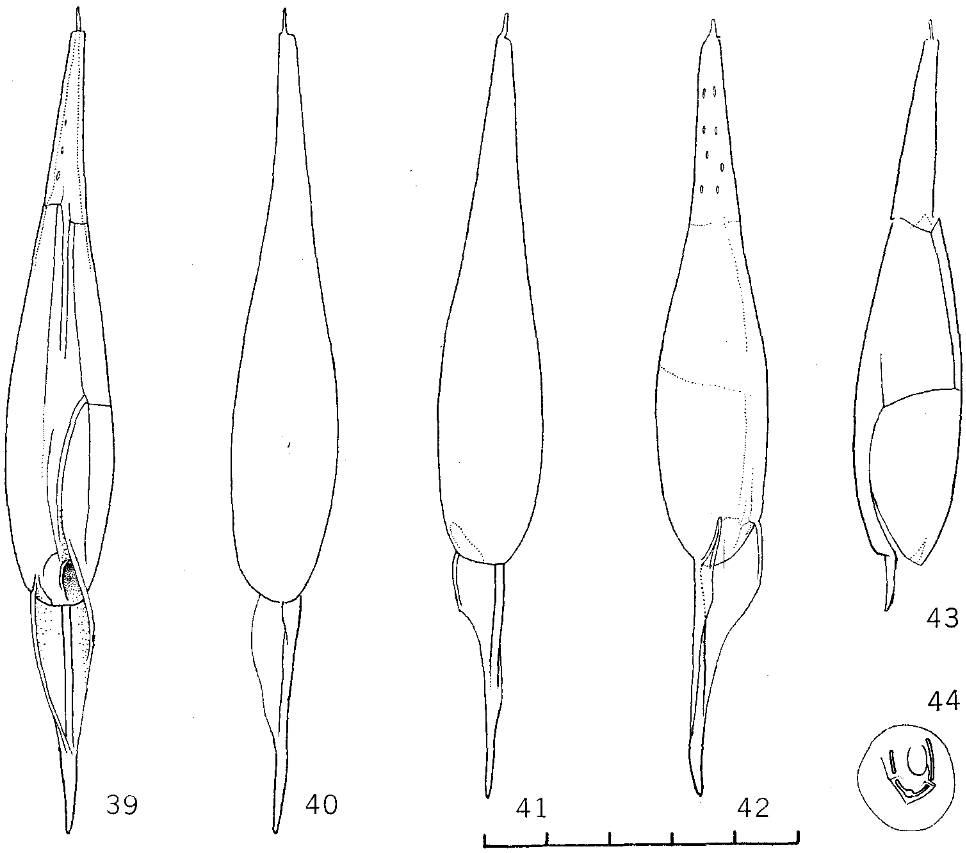
Whether or not the antapical appendage consists of a single or double set seems superficially a problem of quantity, but in reality it is a qualitative problem. In the mono-spiny *spinifera* species, the centre of structure of a winged spine is restricted in the region occupied by the intrinsically posterior sulcal plate, while in the dispinous species the centre of structure is found within the portions destined to be the antapical plates. Taking this into consideration, it seems most reasonable to subdivide the genus *Podolampas* into two, *spinifera* and *bipes* groups. The question whether or not these two groups deserve respectively a generic status is now left unsettled, as the author has many parallel examples to be elucidated in my forth-coming papers.

Podolampas spinifera OKAMURA

(Figs. 39-44)

Podolampas spinifera OKAMURA, 1912, Pl. 1, Figs. 35, 36.
Syn.: *Podolampas spinifer*, PAVILLARD 1916, p. 41, Pl. 2, Figs. 6, 7: SCHILLER 1931, p. 476: BALECH 1963, p. 14, Pl. 2, Figs. 28-33.

This slender species is so translucent and its thecal wall is so thin that morphological study of its thecal structures has not been done in detail. BALECH (1963) was the first who tried to analyse them, though incompletely. Its body is subdivided into three parts of subequal length by the apical-precingular and the precingular-postcingular circular sutures. There is a single antapical triangular wing supported with a median solid spine, which is, in antapical view, U-shaped and consists of one median and two bilateral parts (Fig. 44). By taking this into consideration the elongated three pieces in BALECH's Fig. 33 can easily be elucidated as representing two antapicals and one posterior sulcal. The flagellar pore lies at the left ventral base of the spine, and the left half of the wing bends distally towards the median, coming to cover the flagellar pore and the proximal longitudinally extending portion of the cingular flagellum. The arced anterior sulcal and the left ventral postcingular are illustrated in Fig. 39, and the mojor dorsal postcingular 2‴ and longitudinal bilateral sides of the precingular 2″ in Fig. 43. In the



Flgs. 39-44. *Podolampas spinifera*: Fig. 39. Ventral view. Fig. 40. Left side view. Fig. 41. Left dorsal view. Fig. 42. Right ventral view. Fig. 43. Left dorsal view of a partially broken specimen. Fig. 44. Antapical view showing the flagellar pore and the bases of the antapical spine and its side wing, consisting of three distinct parts.

specimen shown in Fig. 43 the anterior intercalary was broken off when the body was bent dorsally.

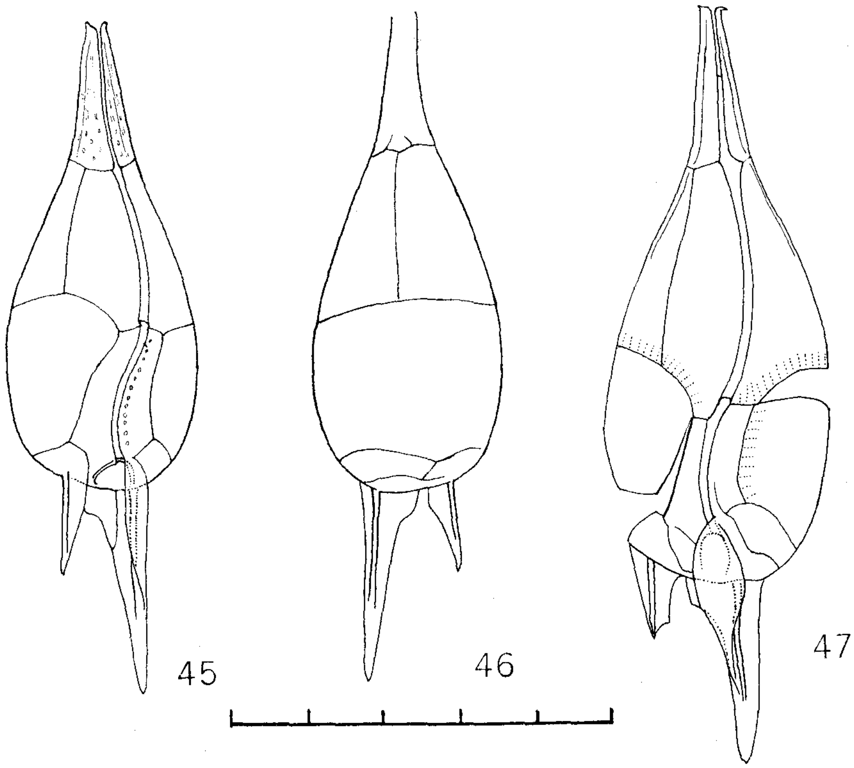
Dimensions: Length of body, 84–92 μ. Greatest transverse dimensions, 16–18 μ. Length of antapical spine, 36–38 μ.

The present species was reported by Okamura (1912) from the south-east temperate waters of Japan, by Pavillard (1916) from the Mediterranean, and fairly recently by BALECH(1963) from Mar del Plata in the Atlantic. The other monospiny species, *curvatus* SCHILLER is too incompletely known to be discussed here.

Podolampas palmipes STEIN

(Figs. 45-51)

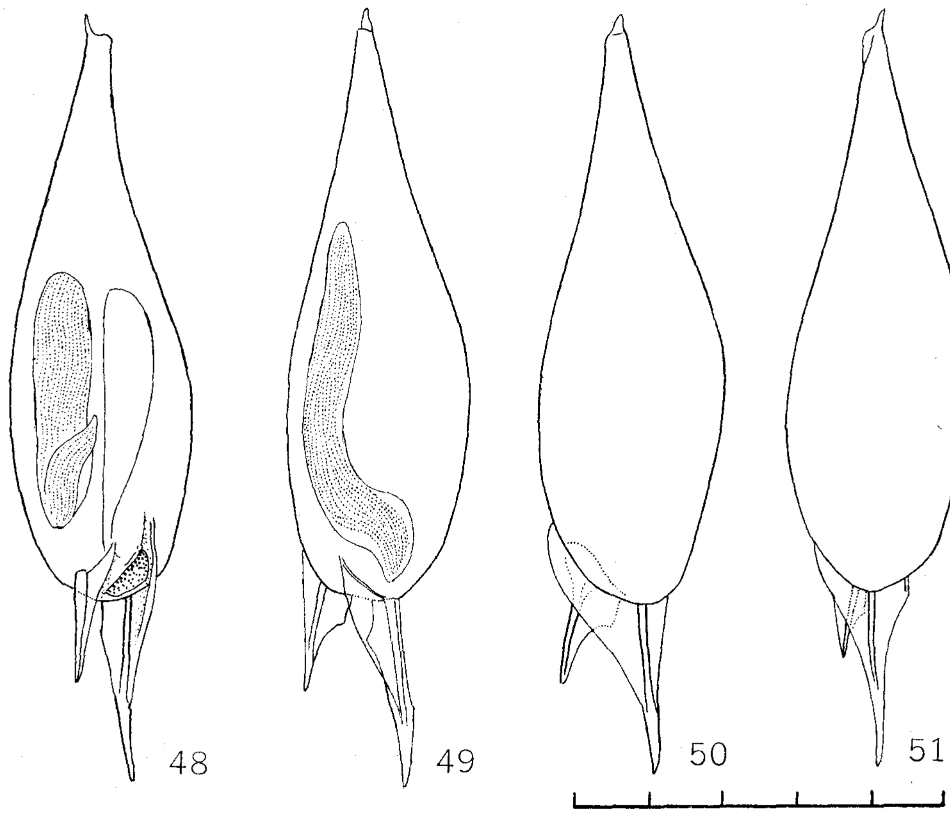
STEIN 1883, Pl. 8, Figs. 9-11: BÜTSCHLI 1889, Pl. 55, Fig. 96: SCHÜTT, 1895, Pl. 18, Fig. 58 *1-8*: ENTZ 1905, Figs. 61-63: PAULSEN 1908, p. 92, Fig. 24: OKAMURA 1912, Pl. 2, Fig. 36: LEBOUR 1925, partim, p. 150, Fig. 52a (left figure): SCHILLER 1937, p. 475, Fig. 475 a, b: Gaarder 1954, p. 57, Fig. 74: BALECH 1963, p. 12, Pl. 2, Figs. 20-27.



Figs. 45-47. *Podolampas palmipes*: Fig. 45. Ventral view. Fig. 46. Dorsal view. Fig. 47. Ventral view of a larger specimen, partially dissociated by pressure given from above coverglass by dint of a needle-point.

The body is slender bottle-shaped with a distally truncated conical anterior half and a rounded posterior furnished with longer left and shorter right antapical appendages. The body is in most cases bilaterally and dorsoventrally symmetrical in shape, but often asymmetrical due to bulging out of its thecal wall in its sinistro-dorsal region (Figs. 48-51). Judging from

Schiller's (1937) form representing an intermediate one between them, these two may be different forms of one species. In any case, however, the two antapical appendages are distinct from each other. The cingular sutural plain tilts down ventrally so that the epitheca occupies the anterior two-thirds on the midventral and the anterior four-sevenths on the dorsal of the



Figs. 48–51. *Podolampas palmipes* of the irregularly-shaped type : Fig. 48. Left ventral view of a living specimen, showing a nucleus on the right and a longitudinally elongated pusule on the median, which opens posteriorly to the canal leading to the flagellar pore. Fig. 49. Left ventral view of another specimen with an elongated nucleus. Fig. 50. Left ventral view of a different specimen with a well buit ventral wing of the left antapical appendage. Fig. 51. Left side view of another specimen. In all of these four specimens, a minute extension can be seen at the apical end. This representes a middorsal portion of an apical collar encircling the apical pore.

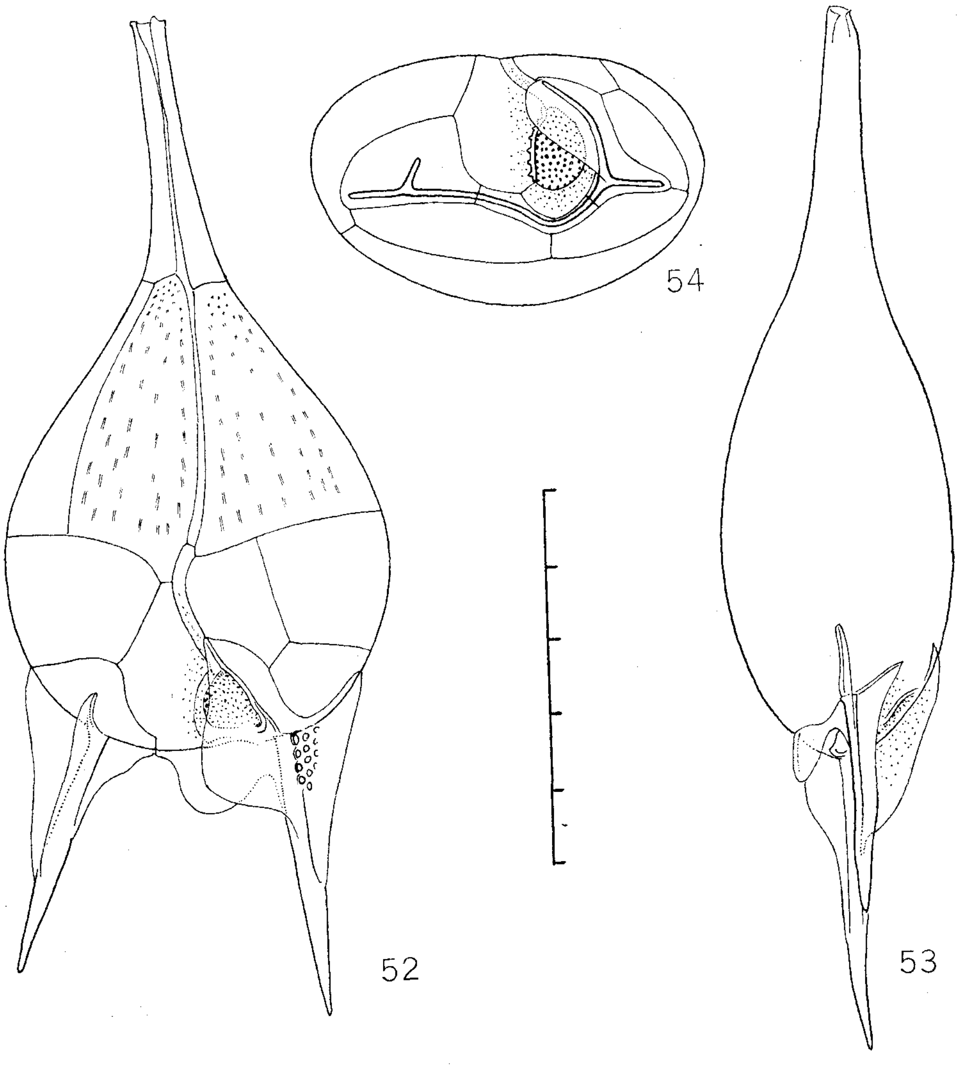
body length. The bilateral apicals are a little shorter than the precingulars. The narrow ventral apical shows, together with the anterior sulcal plate, an elegantly curved sigmoid tract. The right sulcal is subequal in breadth with the left ventral postcingular which is, however, a little shorter. The pore band is distinctly differentiated just as in *P. bipes*.

Dimensions: Length of body, 60–75 μ. Transverse dimension, 25–28 μ. Length of antapical appendages, 24–27 μ.

Distribution: Subtropic and warm temperate waters in both the Pacific and Atlantic.

Podolampas elegans SCHÜTT

(Figs. 52–54)



Figs. 52–54. *Podolampas elegans*: Fig. 52. Ventral view. Fig. 53. Right side view. Fig. 54. Antapical view. It is to be noted, regarding Figs. 52 & 54 that the median wings of the antapical appendages are continuously built and not interrupted at the suture between right-antapical and posterior sulcal plates as in *palmipes* or *bipes*.

SCHÜTT 1895, Pl. 18, Fig. 57: LEBOUR 1925, Fig. 53: KOFOID 1909, pp. 48-60, Pl. 3, Figs. 1-7: SCHILLER 1937, p. 475, Fig. 546: Gaarder 1954, p. 55, Fig. 73 a-e.
Syn.: *Podolampas palmipes*, LEBOUR 1925, partim, Fig. 52a (right figure).

This was the first species of the genus, which was morphologically analysed by KOFOID (1909). It is characterized by a bilaterally bulged mid-body, the elongated conical apical horn and a low but uninterrupted antapical wing. This antapical wing consists of two median side-wings of the two antapical appendages which distinctly diverge distally and have rather a greater length as compared to the body length.

Dimensions: Length of body, 100-106 μ. Transverse diameter, 52-54 μ. Dorso-ventral diameter, 40-43 μ. Length of antapical appendage, 34-42 μ.

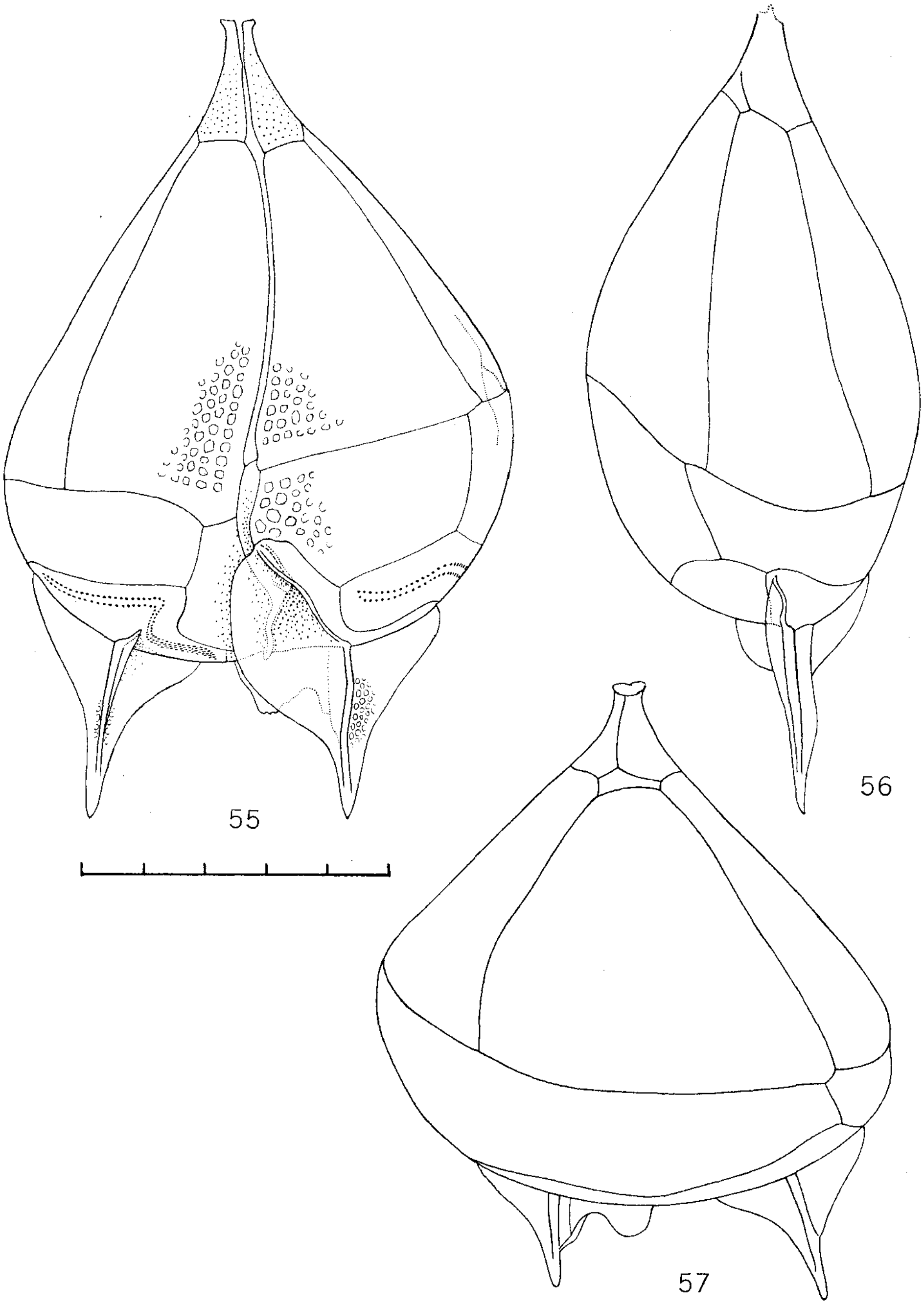
Distribution: Pacific, Mediterranean and Atlantic warm temperate waters.

Podolampas bipes STEIN

(Figs. 55-68)

Podolampas bipes STEIN 1883, Pl. 8, Figs. 6, 7: BÜTSCHLI 1885, Pl. 55, Fig. 9a: SCHÜTT 1895, Pl. 18, Fig. 96; 1896, p.23, Fig. 33; 1899, Pl. 6, Figs. 13-16, Pl. 7, Figs. 19-22, Pl. 8, Fig. 22: ENTZ, G. jun. 1903, Figs. 61, 62: PAULSEN 1908, p. 92, Fig. 125: OKAMURA 1912, Pl. 2, Fig. 37: LEBOUR 1925, p. 160, Fig. 25b: SCHILLER 1937, p. 474: BALECH, 1963, p. 9-11, Figs. 8-11.
Syn.: *Podolampas reticulata* KOFOID 1907, p. 187, Pl. 2, Fig. 11: BALECH 1963, p. 11, Pl. 2, Figs. 15-19.
Podolampas bipes, forma *reticulata* (KOF.) SCHILLER 1937, p. 474.

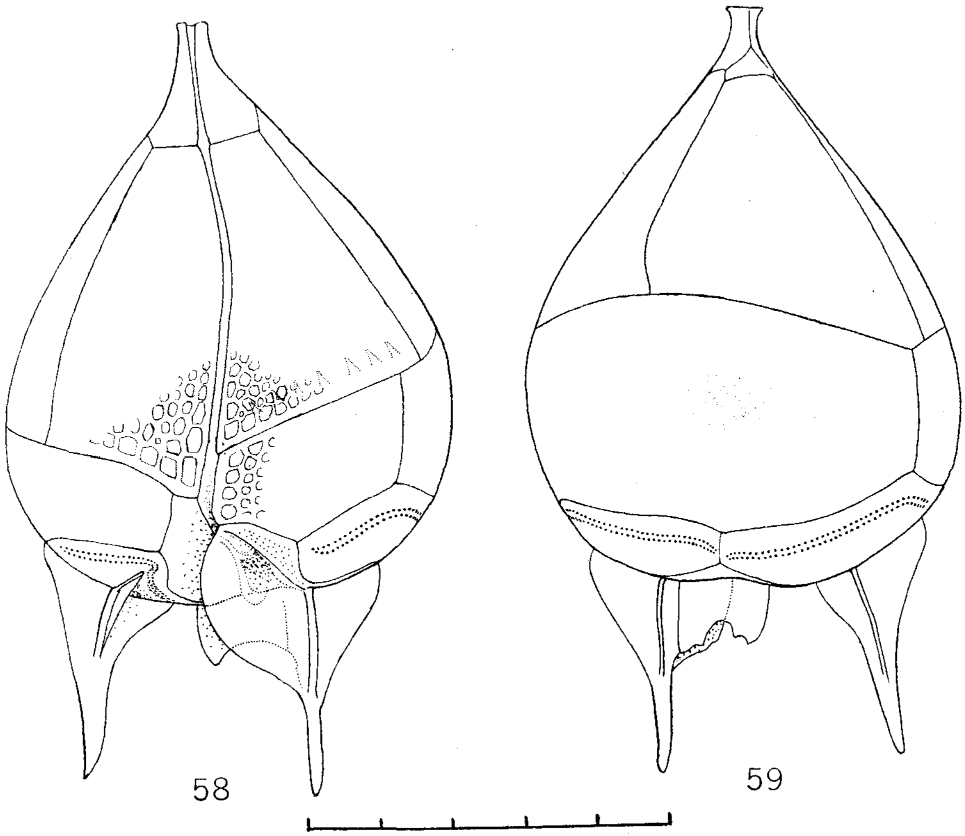
KOFOID (1907) distinguished *reticulata* from *bipes* mainly by its "very large and broadly rounded" antapical fins and its reticulated thecal surface. The present author found from Shimoda Bay some intermediate forms in addition to the two typical ones. In respect to the surface reticulation, all of the above-mentioned forms cannot be distinguished from one another. The sole difference to be mentined is in the structural relations of the antapical appendage. In the *bipes*--type specimens, all of the three side-wings can be traced almost to the distal end of the spine, while in the intermediate forms the side-wings are restricted to the basal half or a little more limited portion of the spine, although they are similarly triangular in shape. In *reticulata*-form collected from Shimoda Bay (Figs. 60-62), the spines are much shorter, hardly extending beyond the side-wings which are roughly truncated at the distal end bearing along their free margin one to several serrae. In KOFOID's (1907) figure this serration along their free margin is much less distinctly illustrated. Areolation of the wings is seen in the *bipes*-type. If based on the structural relations of the appendage, these types can be arranged in the order of intermediate from, *bipes*--type and *reticulata*-type. They agree with one another also in the plate pattern of the body surface. It seems to the



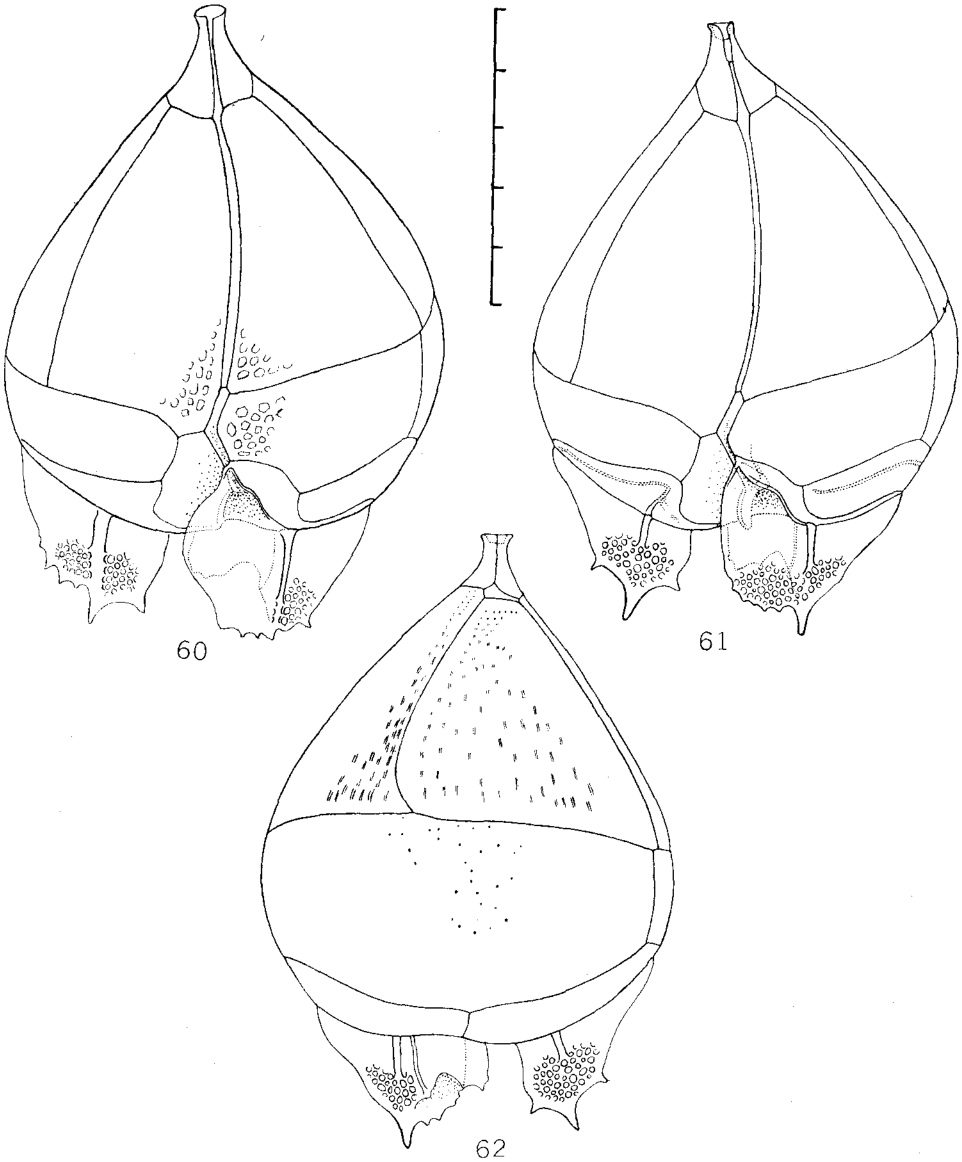
Figs. 55–57. *Podolampas bipes* : Fig. 55. Ventral view of a typical specimen. Fig. 56. Right-anterior view. Fig. 57. Dorso-anterior view.

author highly probable that these three forms are within the range of individual variations. This may be supported by the fact that this species is recorded not only from the warm temperate waters but not infrequently from fairly cold water regions, too.

Dimensions: Length of body, 80–115 μ. Transverse dimension, 60–84 μ. Dorso-ventral dimension, 43–56 μ. Length of appendage, 26–31 μ.



Figs. 58–59. *Podolampas bipes* of the long-spined type: Fig. 58. Ventral view. Fig. 59. Dorsal view.



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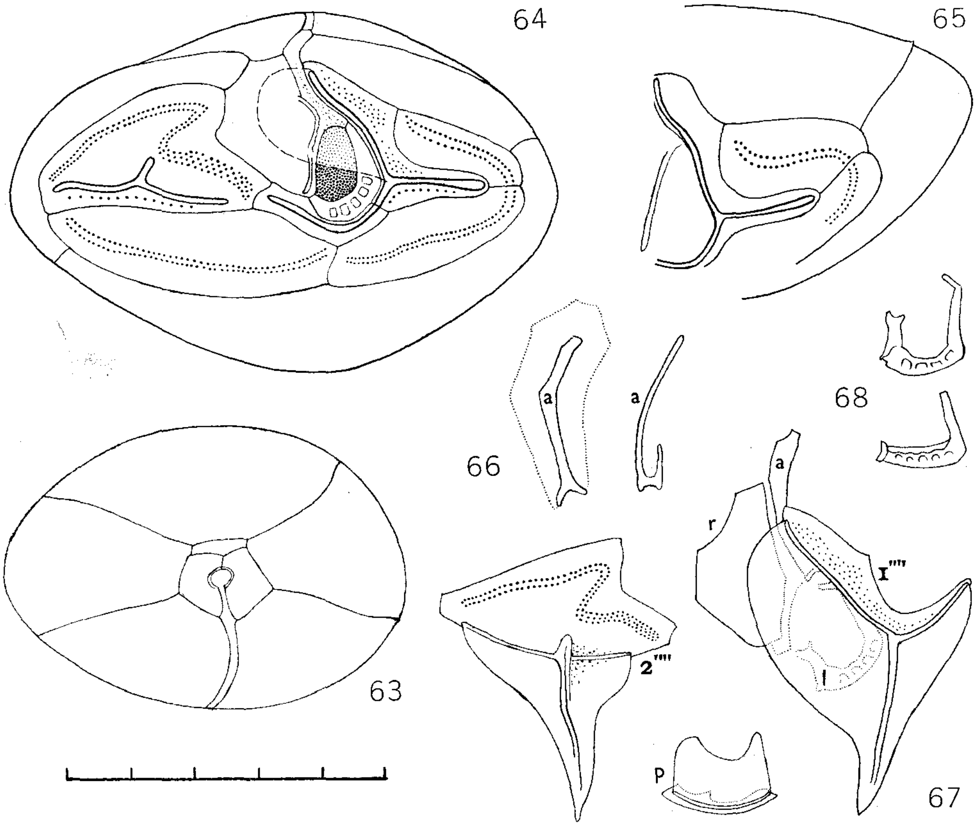
Figs. 60–62. *Podolampas bipes* of *reticulata*-type : Fig. 60. Ventral view. Fig. 61. Ventral view of another specimen, Fig. 62. Dorsal view of the specimen shown in Fig. 61.



Figs. 63–68. *Podolampas bipes* : Fig. 63. Apical view. Fig. 64. Antapical view of a larger specimen. Fig. 65. Left antapical portion of a different specimen, showing relationships between the two postcingulars, the left two intercalaries and the left antapical, and especially the site and arrangement of the left ventral portion of the specially differentiated row of rather larger pores. Fig. 66. Ventral and side views of the same anterior sulcal plate, on the left is shown its marginal thinner edge which underlies its adjoining thecal plates. Fig. 67. Completely separated two right antapical plate, posterior sulcal plate with a transversely formed surface wing (p) and left antapical plate ($1''''$), to which are adhered, though loosely, anterior (a), left (l) and right (r) sulcal plates. Fig. 68. The posterior sulcal plate, isolated from two different specimens. One is typically L-shaped while the other is asymmetrically U-shaped ; the latter may be due to a stronger development of the marginal edge extending along the under-surface of the adjoining right sulcal plate.

All drawings from Fig. 7 to Fig. 68 were made by means of camera lucida.